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# Plant Water Deficits, Osmotic Properties, and Hydraulic Resistances of Hawaiian *Dubautia* Species from Adjacent Bog and Wet-Forest Habitats[1]

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ABSTRACT: Functional responses of two closely related *Dubautia* species from a mosaic of Hawaiian bogs and wet forest were compared to help explain their differential distributions. *Dubautia paleata* is largely restricted to saturated bogs, while *D. raillardioides* is restricted to the surrounding, better-drained wet forest. Minimum diurnal tissue water potentials of *D. paleata* are significantly lower than those of *D. raillardioides*, despite the moister condition of bog soil. The tissue osmotic potential at full hydration ($\pi_i$) of *D. paleata* is significantly lower than that of *D. raillardioides*. As a result, the tissue water potential at which turgor reaches zero for *D. paleata* is significantly lower than that of *D. raillardioides*. *Dubautia paleata* is thus able to maintain positive turgor to lower water potentials than *D. raillardioides*. Lack of a lowered $\pi_i$ in *D. raillardioides* may therefore contribute to exclusion of that species from the bog habitat. Preliminary data suggest a significantly greater hydraulic resistance for *D. paleata* than for *D. raillardioides*, probably due to higher root resistance caused by the reduced condition of the waterlogged bog substrate. The difference in hydraulic resistance could help account for the contrasting water deficits of the two species.

AS ONE OF THE WETTEST terrestrial habitats, bogs would not be expected to cause substantial tissue water deficits in plants. However, moderately low tissue water potentials (−1.5 to −2 MPa) have been reported for temperate and subarctic bog species (Small 1972, Johansson and Linder 1975, Marchand 1975). Although these minima are not nearly as low as those reported for xerophytes, they nevertheless may affect metabolic processes adversely (Hsiao et al. 1976).

One probable cause of low water potentials in bog plants is the saturated soil. Hypoxia inhibits root respiration, reducing the viable root mass (Bannister 1964, Cook et al. 1980). Appreciable root resistance can thus develop, creating substantial hydraulic resistance in bog plants (Marchand 1975, Bradbury and Grace 1983).

One physiological mechanism capable of buffering the effect of tissue water deficits is a decrease in tissue osmotic potential. A lowered osmotic potential enables turgor to be maintained to lower tissue water contents (Tyree and Jarvis 1982). Stomatal opening and photosynthetic carbon assimilation are among the physiological processes adversely affected by water deficits. Whether moderate water deficits are transduced into metabolic changes through a reduction in turgor pressure is still a matter of debate (Hsiao et al. 1976, Turner and Jones 1980, Schulze 1986). It has been argued that the ability of plants to maintain turgor at lower tissue water contents may promote their growth and survival under moisture-limited conditions (Turner and Jones 1980, Bradford and Hsiao 1982). Low osmotic potentials (e.g., −3 MPa) have been reported for bog plants (Harris 1934, Ingram 1983).

This paper addresses the water status of bog plants by examining two closely related species of *Dubautia* (Asteraceae) from adjacent

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bog and wet-forest habitats in Hawaii. The extent to which these plants develop tissue water deficits is described first. The osmotic properties of the species are discussed, along with the potential effect of those properties on turgor maintenance. Finally, limited hydraulic resistance data are related to the contrasting water deficits of the two species.

## MATERIALS AND METHODS

*Dubautia paleata* Gray and *D. raillardioides* Hbd. are endemic to the Hawaiian island of Kauai. They are most common in the central upland portion of Kauai known as the Alakai Swamp, a dissected plateau of wet forest and open bogs within the montane rainforest zone. Located at 1200–1600 m elevation, the Alakai plateau receives abundant orographic precipitation brought by the prevailing northeast tradewinds. The average annual rainfall ranges from 2500 to 11,500 mm and is not markedly seasonal (State of Hawaii 1982).

The study site, Aipo Iki bog along the Alakai Swamp Trail (1222 m elevation; 3200 mm annual rainfall), is a typical open to shrubby, nearly flat, poorly drained bog surrounded by low-stature wet forest near better-drained slopes. In both habitats *Metrosideros polymorpha* (Myrtaceae) is dominant. The profusion of epiphytic ferns and bryophytes attests to the prevalence of rain and fog at the site. Highly acidic, saturated peat forms the bog substrate. In the adjacent forest the soil water content averages half that of the bog, and the rhizosphere is typically three times as deep as in the bog (Canfield 1986).

*Dubautia paleata* is a small shrub, averaging 0.5 m in height, and is primarily restricted to the bog. *Dubautia raillardioides* is a large, sprawling shrub, often reaching a height of 2 m, and is confined to the understory of the wet forest. Because the boundary between the two habitats is rather sharp, individuals of the two species can be found growing within 20 m of each other.

Diurnal tissue water potentials of the two species were determined during the summer of 1983 and spring, summer, and winter of 1984 with a PMS Instrument Co. model 1000 pressure chamber.

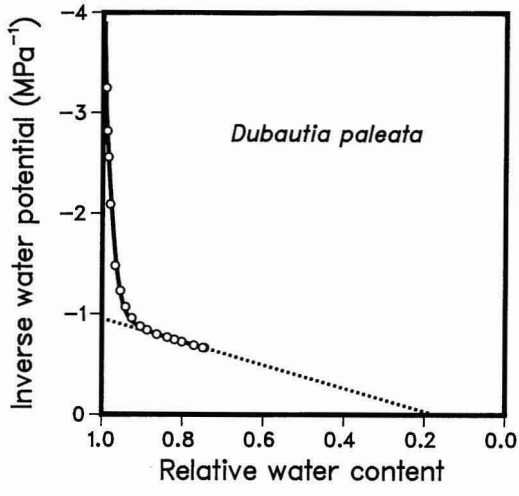


FIGURE 1. The reciprocal of tissue water potential as a function of tissue relative water content for a branch of *D. paleata*. One additional point extends the curve higher on the ordinate than shown here. The correlation coefficient for the linear region of the curve (defined by seven data points) is 0.999.

Tissue osmotic properties were determined by the pressure chamber technique (Tyree and Jarvis 1982, Robichaux 1984). Sets of branches were collected during the summer and winter of 1983 and the spring and summer of 1984. After being recut under water in the laboratory, the branches were stored overnight in distilled water to restore turgor. Repeated measurements of weight and water potential were made as the branches dried out, following the procedure of Robichaux (1984). Dry weight of the branches was obtained after oven drying for 24 hr at 70–80° C. Weights were measured with a Sartorius GmbH model 1212MP digital balance.

The relative water content of each branch was calculated as described by Robichaux (1984). The inverse of tissue water potential was then plotted as a function of relative water content (Figure 1). Extrapolation of the linear part of the resulting curve to the ordinate gives the reciprocal of the osmotic potential at full hydration (Tyree and Jarvis 1982). The difference between the values of water potential (on the curve) and osmotic potential (on the extrapolated line) for a given value of relative water content is equivalent to the tissue turgor pressure (Tyree and Jarvis 1982).

Hydraulic resistances to liquid water flux in the soil-root-shoot continuum were calculated for five to six branches of each species on 16 July 1985 with the following formula: $R = (\psi_{branch} - \psi_{soil})/E$, where $R$ is hydraulic resistance, $\psi_{branch}$ and $\psi_{soil}$ are tissue and soil water potentials, respectively, and $E$ is transpiration (Cowan 1977, Calkin and Pearcy 1984). This formula makes the assumption that $E$ can be used as an estimate of the liquid water flux supplied per unit area of leaf by the soil-root-shoot continuum (Calkin and Pearcy 1984). $\psi_{soil}$ was determined with a Soil-moisture Equipment Co. model 1500 ceramic plate extractor. Values of $\psi_{soil}$ were $> -0.01$ MPa for both species.

$E$ was calculated according to Cowan (1977) and Hall and Schulze (1980) except for the boundary layer resistance to water vapor ($r_b$). $r_b$ was calculated as $[0.4(d/u)^{-0.5}]/D$, where $d$ is leaf width, $u$ is wind speed, and $D$ is the diffusion coefficient of water vapor (Campbell 1977, Nobel 1983). Wind speeds were measured with a Weather Measure Corp. model W131 anemometer.

For the calculation of $E$, leaf resistances to water vapor were measured with a LI-Cor Inc. model LI-1600 steady-state porometer. Leaf temperatures were measured with fine-wire (0.076 mm) copper-constantan thermocouples appressed to the abaxial leaf surfaces and connected to a Wescor Inc. model TH-65 digital thermocouple thermometer. The resistances and temperatures of three to four leaves of each branch were measured immediately before determining the water potential of that branch. Atmospheric humidity was measured with the porometer's humidity sensor and was less than 80% during the measurements. Student's $t$ test was used for all statistical analyses.

## RESULTS

The diurnal tissue water potential of *D. paleata* growing in the bog consistently fell lower than that of *D. raillardioides* in the wet forest (Figure 2). The minimum diurnal water potentials ($\psi_{min}$) of the two species were significantly different for each of the four sampling dates given in Table 1. For the entire sampling

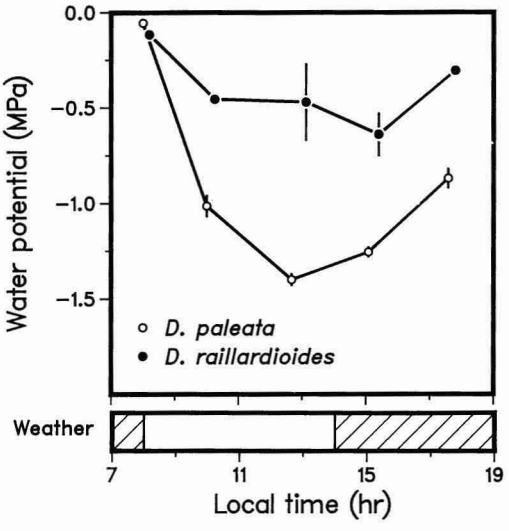


FIGURE 2. Diurnal tissue water potentials of *D. paleata* from Aipo Iki bog and *D. raillardioides* from the adjacent wet forest on 25 March 1984. Vertical lines show the range of variation for duplicates, where not eclipsed by the symbol. Weather conditions indicated at bottom are partly cloudy (shaded) or clear and sunny (not shaded).

period, the mean value of $\psi_{min}$ for *D. paleata* ($-1.07 \pm 0.13$ MPa) was significantly lower ($P < 0.001$) than that of *D. raillardioides* ($-0.47 \pm 0.17$ MPa). Maximum tissue water potentials ($\psi_{max}$) of *D. paleata* were the same as or slightly higher than those of *D. raillardioides* (Table 1). Over the whole sampling period, the mean value of $\psi_{max}$ was $-0.03 \pm 0.01$ MPa for *D. paleata* and $-0.08 \pm 0.02$ MPa for *D. raillardioides*. The bog species thus showed a significantly greater total diurnal range in $\psi$ than its wet-forest relative.

The two species showed a consistently significant difference in tissue osmotic potential at full hydration ($\pi_i$) (Table 1). The mean value of $\pi_i$ for *D. paleata* over the entire sampling period was $-1.06 \pm 0.01$ MPa; that for *D. raillardioides* was $-0.77 \pm 0.02$ MPa. The value of $\pi_i$ for the bog species was thus significantly lower ($P < 0.001$) than that of the wet-forest species.

The effect on turgor of the difference in $\pi_i$ of the two species is apparent from a plot of tissue turgor pressure ($P$) as a function of $\psi$ (Figure 3). The difference in $P$ for the two species at maximal hydration (equal to the difference in their values of $\pi_i$) continued at

TABLE 1

MAXIMUM AND MINIMUM DIURNAL TISSUE WATER POTENTIALS ($\psi_{max}$, $\psi_{min}$), TISSUE OSMOTIC POTENTIALS AT FULL HYDRATION ($\pi_i$), TISSUE WATER POTENTIALS AT ZERO TURGOR ($\psi_0$), AND SAMPLE SIZE ($n$) FOR *Dubautia paleata* AND *D. raillardioides* AT AIPO IKI

| | | $\psi_{max}$ | | $\psi_{min}$ | | $\pi_i$ | | $\psi_0$ | |
|---|---|---|---|---|---|---|---|---|---|
| DATE | SPECIES | (MPa) | $n$ | (MPa) | $n$ | (MPa) | $n$ | (MPa) | $n$ |
| August 1983 | *D. paleata* | −0.04a (0.01) | 4 | −0.82b (0.04) | 4 | −1.10 | 2 | −1.36 | 2 |
| | *D. raillardioides* | −0.07a (0.02) | 4 | −0.23 (0.07) | 4 | −0.71 | 2 | −0.94 | 2 |
| January 1984* | *D. paleata* | −0.02 | 2 | −1.15 (0.03) | 4 | −1.06 (0.01) | 7 | −1.32 (0.01) | 7 |
| | *D. raillardioides* | −0.02 | 2 | −0.30 (0.07) | 4 | −0.73 (0.01) | 6 | −0.85 (0.02) | 6 |
| March 1984 | *D. paleata* | −0.06 | 2 | −1.40 | 2 | −1.10 (0.01) | 6 | −1.33 (0.02) | 6 |
| | *D. raillardioides* | −0.12 | 2 | −0.64 | 2 | — | — | — | — |
| June 1984 | *D. paleata* | −0.02 | 2 | −1.07 (0.03) | 6 | −1.03 (0.02) | 6 | −1.26 (0.02) | 6 |
| | *D. raillardioides* | −0.07a (0.05) | 3 | −0.67b (0.04) | 6 | −0.83 (0.01) | 6 | −0.97 (0.01) | 6 |

NOTE: Standard errors are given in parentheses for all $n > 2$. Comparisons with $n > 2$ between species in a given column followed by a common letter are not significantly different. All other comparisons are significantly different ($P < 0.05$).

* $\psi_{max}$ and $\psi_{min}$ are from December 1984.

lower values of $P$ and $\psi$. For example, at $\psi = -0.8$ MPa in Figure 3, the value of $P$ for *D. raillardioides* was 1/10 that of *D. paleata* (0.02 versus 0.3 MPa).

A further result of the contrast in osmotic values of the two species is that the value of $\psi$ at which $P$ reaches zero ($\psi_0$) was significantly lower in *D. paleata* than in *D. raillardioides* (Table 1). For the branches reported in Figure 3, $\psi_0$ for *D. paleata* was −1.30 MPa, while that for *D. raillardioides* was −0.84 MPa. For the bog species, $\psi_0$ averaged $-1.31 \pm 0.01$ MPa throughout the sampling period; for the wet-forest species, the mean value was $-0.91 \pm 0.02$ MPa, significantly higher ($P < 0.001$) than that of *D. paleata*.

The significance of these osmotic differences can be illustrated by comparing values of diurnal $\psi$ sustained by *D. paleata* with values of $\psi_0$ for *D. raillardioides*. Table 1 shows that values of $\psi_{min}$ for *D. paleata* fall below the point of zero turgor ($\psi_0$) for *D. raillardioides* in both January and June. In other words, if *D. raillardioides* were growing in the bog and sustained diurnal water potentials typical of *D. paleata*, its branches would lack turgor for a considerable part of the day. This is also apparent if values of $\psi_0$ for *D. raillardioides* from Table 1 are applied to the diurnal $\psi$ curve for *D. paleata* in Figure 2.

$\Delta\psi$ ($\psi_{branch} - \psi_{soil}$) is significantly lower for *D. paleata* than for *D. raillardioides* (Table 2). Leaf resistances to water vapor ($r_l$) and $E$ are significantly higher for *D. paleata* than for its wet-forest congener (Table 2). Hydraulic resistances calculated for the single sample time are also significantly higher for *D. paleata* than for *D. raillardioides* (Table 2).

## DISCUSSION

Diurnal tissue water potentials of *D. paleata* are similar to those reported for shrubs from temperate and subarctic bogs (Small 1972, Johansson and Linder 1975, Marchand 1975). As is true of other bog shrubs, the value of $\psi_{min}$ for *D. paleata* is

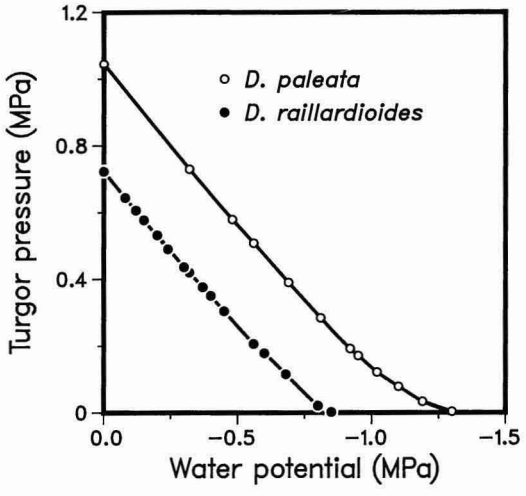


FIGURE 3. Relationship between tissue turgor pressure ($P$) and tissue water potential for *D. paleata* and *D. raillardioides* from Aipo Iki in January 1984. Values of $P$ at full turgor are equal (but with the opposite sign) to the osmotic potentials at full hydration.

moderately low, despite the abundance of moisture in the bog habitat. Although slightly higher than values of $\psi_{min}$ reported from temperate bogs, the minima reported here are within the range normally resulting in deleterious effects on metabolic processes (Hsiao et al. 1976). Lower values of $\psi_{min}$ in boggy sites than in better-drained, adjacent sites have also been found for closely related species pairs in New England (Marchand 1975). Because they reflect greater tissue water deficits, these results indicate that, in terms of plant water status, bogs are more extreme environments than less-saturated adjoining habitats.

The significantly lower value of $\pi_i$ for *D. paleata* relative to *D. raillardioides* translates into a higher value of $P$ at a given value of $\psi$. Differences in tissue elastic properties apparently do not contribute to turgor maintenance in these two *Dubautia* species. The tissue elastic modulus near full hydration, calculated as described by Robichaux (1984), does not differ significantly for the two species over the sampling period, as indicated by the similar slope of the lines in Figure 3.

The physiological effect of waterlogging on the species is suggested by the variation in tissue osmotic properties under wetter and drier conditions. *Dubautia paleata* shows a consistent pattern of lower $\pi_i$ and $\psi_0$ under wetter substrate conditions. If $R$ is greater under waterlogged conditions because of root resistance, then a lowered $\pi_i$ and $\psi_0$ would minimize the effect of internal water deficits on turgor. *Dubautia raillardioides* shows the opposite pattern in its osmotic properties, corresponding to osmotic adjustment, which contributes to turgor maintenance in many plants from moisture-limited environments (Hsiao et al. 1976, Turner and Jones 1980, Morgan 1984).

The contrasting osmotic properties of these two species may play a role in their distribution. Because of the difference in $\psi_0$ of the species, *D. raillardioides* would sustain zero turgor for prolonged periods were it to experience the diurnal $\psi$ of its close relative in the

TABLE 2

WATER POTENTIAL GRADIENTS ($\Delta\psi$), LEAF RESISTANCES TO WATER VAPOR ($r_l$), BOUNDARY LAYER RESISTANCES TO WATER VAPOR ($r_b$), TRANSPIRATION ($E$), HYDRAULIC RESISTANCES ($R$), AND SAMPLE SIZE ($n$) FOR *Dubautia paleata* AND *D. raillardioides* AT AIPO IKI ON 16 JULY 1985

| SPECIES | $\Delta\psi$ (MPa) | $r_l$ (cm$^2$ s mmol$^{-1}$) | $r_b$ (s cm$^{-1}$) | $E$ (mmol m$^{-2}$ s$^{-1}$) | $R$ (MPa m$^2$ s mmol$^{-1}$) | $n$ |
|---|---|---|---|---|---|---|
| *D. paleata* | −0.92 (0.03) | 31.20 (3.20) | 0.30 | 4.42 (0.68) | 0.24 (0.03) | 6 |
| *D. raillardioides* | −0.16 (0.01) | 26.59 (1.10) | 0.42 | 1.65 (0.17) | 0.10 (0.01) | 6* |

NOTE: Standard errors are given in parentheses. Figures in all columns with standard errors are significantly different ($P < 0.01$) between species.

*For $\Delta\psi$ and $R$, $n = 5$.

bog. Because leaves of *D. raillardioides* are observed to wilt under temporary conditions of direct irradiance in the wet-forest understory, more prolonged wilting and turgor loss would likely be experienced were it growing in the open bog. The lack of a lowered $\pi_i$ to buffer the effects of high $\Delta\psi$ and $R$ in the bog may thus contribute to the exclusion of *D. raillardioides* from the open-bog habitat.

$R$ was calculated to investigate underlying causes of the difference in water deficits between the two species. Taken at only one point in time, these data are somewhat limited: Calkin and Pearcy (1984) and Koide (1985) have found $R$ to vary with $E$.

The contrasting values of $R$ for the two *Dubautia* species are reflected in contrasting values of $E$, influenced by differences in $r_l$ and leaf temperature. To a certain extent, the difference in $R$ must be due to environmental effects on $E$ that differ between the two habitats. Other possible causes of the interspecific difference in $E$ include differing nutritional needs or differing stomatal sensitivity.

In other studies (Koide 1985), including interspecific comparisons (Calkin and Pearcy 1984), higher $E$ is correlated with lower $R$. However, *D. paleata*'s higher value of $E$, relative to *D. raillardioides*, is correlated with a higher $R$. Opposing the typical pattern, this suggests a real difference in $R$ between these two species.

The considerable difference in $\Delta\psi$ also supports a real difference in $R$ between the *Dubautia* species. The sixfold discrepancy in $\Delta\psi$ indicates that *D. paleata* requires a far greater driving force to maintain its internal water supply than *D. raillardioides*. This suggests that the bog species must encounter much greater resistance along the soil-root-shoot pathway. Alternatively, it is possible that $R$ is affected by the ratio of evaporative demand to supply. A higher ratio of leaf mass to root conductive surface in *D. paleata* could result in a larger $\Delta\psi$.

The pattern of greater $R$ for the bog *Dubautia* species than for its wet-forest relative parallels Marchand's (1975) finding for the flow resistances of four species growing in both a bog and an adjacent upland. Küppers (1984) implicated high $R$ in the exclusion of a shrub species from an open habitat.

In the saturated substrate where *D. paleata* grows, resistance at the soil-root interface is a likely source of higher $R$, as suggested in other bog studies (Marchand 1975, Bradbury and Grace 1983). At this rather oligotrophic Hawaiian bog, the low oxidation-reduction potential (Eh = 560 mV at soil pH, indicating hypoxia, reduced Fe and Mn, and other toxic ions), very low soil pH (3.8), and extremely high soil water content (1200% of soil dry weight) indicate the likelihood of high soil-root and root resistances (Canfield 1986). Differences in $R$ may thus help account for the contrasting water deficits of the two species.

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